EMERGENCE, ATTACK DENSITIES, AND HOST RELATIONSHIPS FOR THE DOUGLAS-FIR BEETLE (*DENDROCTONUS PSEUDOTSUGAE* HOPKINS) IN NORTHERN COLORADO

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ABSTRACT.—Douglas-fir beetle–infested Douglas-fir trees were partially caged to determine the emergence period and beetle production. Beetles began emerging in April, but emergence peaked between 10 and 26 June. In 1987 and 1988 beetle emergence averaged 20 or more per sq. ft. of bark. Annual growth of the infested trees showed a decline prior to the beetle outbreak followed by an increase during the outbreak.

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is usually an insignificant pest of Douglas-fir (*Pseudotsugae menziesii* [Mirb.] Franco) in the Front Range of Colorado. The beetle's life cycle generally lasts one year, although a partial second generation has been noted in other parts of its range. The beetle prefers windthrown trees but will infest standing trees during droughts or high population levels (Wood 1963). Standing trees also become more susceptible to infestation by the Douglas-fir beetle after severe defoliation by insects (Wright et al. 1984).

In 1972 western spruce budworm (*Choristoneura occidentalis* Freeman) populations began to increase in Roosevelt National Forest west of Fort Collins. Defoliation was noticeable, moderate, and limited to 3500 acres (1378 ha) in 1974 (Minnemeyer 1974), but by 1976, 54,000 acres (21,260 ha) were moderately to severely defoliated. Parts of Poudre Canyon, the location in this study, were severely defoliated (Cresap 1976). In 1977, the area of severe defoliation more than doubled on the forest (115,840 acres [45,606 ha]). Defoliation continually increased from 1977 until 1983, reaching a maximum of 469,000 acres (184,646 ha) (see Raimo 1983). Defoliation in Poudre Canyon, while noted as early as 1976, was confined to particular portions and was not extensive throughout until 1980 (see Linnane 1977, 1981). Thereafter, it was extensive and moderate to severe on most north-facing slopes until 1983–84.

Although the acreage of moderately to severely defoliated stands progressively increased from 1977 to 1983, egg mass densities peaked in 1980, four years prior to the maximum acreage defoliation, and had declined substantially by 1984 (see Raimo 1983, 1984). By 1985 population levels became endemic, with only light defoliation visible.

As the budworm outbreak subsided, Douglas-fir beetle populations began to increase. Scattered groups of faded trees were observed in the mid-1970s. Subsequently, beetle-killed Douglas-fir have increased both in numbers and in geographic extent (J. M. Schmid, personal observation). Numerous stands of Douglas-fir on north-facing slopes suffered significant tree mortality.

Because tree mortality became significant and our knowledge of the life history and habits of the Douglas-fir beetle in Colorado was deficient, the current infestations provided an opportunity to learn more about the beetle's life history and habits in Douglas-fir stands in Colorado and expanded our knowledge of the geographic variation in these aspects of the beetle's biology.

METHODS

To monitor beetle emergence, we attached 1 × 2-ft. (.3 × .6-m) wire screen emergence cages to infested trees in Poudre Canyon west of Fort Collins, Colorado, in late February 1987. Two cages were attached at breast height on each of five randomly selected

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1986-infested trees at each of three locations: the Narrows, Pingree Park road turnoff, and near BM 6998 (east of Indian Meadows). On April 3 another five trees near Crystal Lakes (northwest of Red Feather Lakes) were caged in the same manner.

To monitor emergence in 1988, we attached cages, as described above, to five 1987-infested trees on each of four sites: near Crystal Lakes (northwest of Red Feather Lakes) and in Poudre Canyon in late September 1987, and also near Camman Springs (south of Poudre Canyon) and near Black Mountain (north of Red Feather Lakes) in late October.

Cages were attached at breast height for practical purposes. Furniss (1962) recommended sampling for attack and brood densities at the midpoint on the bole because attack densities were twice as great there as at breast height, attack success was greatest in the midpoint zone, and live brood was greater. Furniss worked on standing trees that averaged 20 inches in diameter at breast height and ranged in height from 79 to 162 ft.; the sampling point on the average tree was thus 40 ft. or more aboveground. In contrast, our trees averaged 15 inches in diameter at breast height with trees only at the Pingree Park road site averaging 20 inches; tree height ranged from 34 to 88 ft. Although Furniss recommended sampling at or near the midpoint of the bole, it should be noted that he felled his trees for sampling and did not extract his samples from standing trees. In addition, the zone of optimum sampling is lower on smaller trees in the southern portion of the trees' range, i.e., southern Utah, than in Idaho, where Furniss did his study. Because our trees were smaller and were not to be felled, the terrain was difficult at some sites, and there was no evidence to suggest that the beetle's emergence pattern varied with height, we attached cages at breast height.

During 1987 and 1988, cages were checked at one- to two-week intervals from 1 April to 1 July. After 1 July, cages were checked at irregular intervals through September. During each check period, the number of emerging adults was recorded for each cage, and observations were made on the discoloration of foliage on the infested trees.

The density of emerging beetles per sq. ft. (.09 m^2) of bark surface was determined by dividing the total number of beetles emerging

in each cage by the surface area covered by each cage (ca. 2 sq. ft. [.18 m^2]). Beetle numbers were subjected to one-way analysis of variance to determine if differences among locations were significant (alpha = .05). Beetle numbers at breast height were also tested against their respective tree diameters to determine if beetle production was related to tree diameter (DBH). For each year, tree diameters were grouped into three classes, and beetle numbers among diameter classes were tested for significant differences using analysis of variance (alpha = .05). For 1987 the diameter classes in inches (cm) were: 7.5–9.6 (19–24), 11.2–15.7 (31–61) and 16.2–24.3 (41–62). For 1988 diameter classes were: 9.3–12.5 (24–32), 12.6–13.3 (32–34), and 13.4–18.0 (34–46). Diameter classes differed between 1987 and 1988 because the diameters of the infested trees were different. A one-way ANOVA was used because all diameter classes were not equally present on all locations.

Population trend was evaluated by dividing the density of emerging beetles by twice the density of attacks (this assumes a pair of beetles creates each attack). When the ratio of emerging beetle density to attack density exceeds one, the beetle population is increasing. When the ratio is less than one, the population is decreasing.

The density of beetle attacks on standing trees was determined by removing 6 × 12-inch (15 × 30-cm) bark samples from or near breast height. Two samples were removed from each 1986-infested tree in late October 1987. Two samples from each 1987-infested tree were removed in late September 1987. The bark samples from 1987-infested trees were also used to determine brood density and stage of development.

To determine past growth rates of the 1986-infested trees, we extracted increment cores from the caged trees at breast height. Annual radial growth for each of the last 20 years was measured to .001 inch (.03 mm). Mean annual growth was determined for all trees from each of the four locations. Annual growth during the three preceding five-year periods (1972–76, 1977–81, 1982–86) was analyzed for significant differences in the periodic growth rate using one-way analysis of variance (alpha = .05). Separate one-way analysis of variance was used for each location because
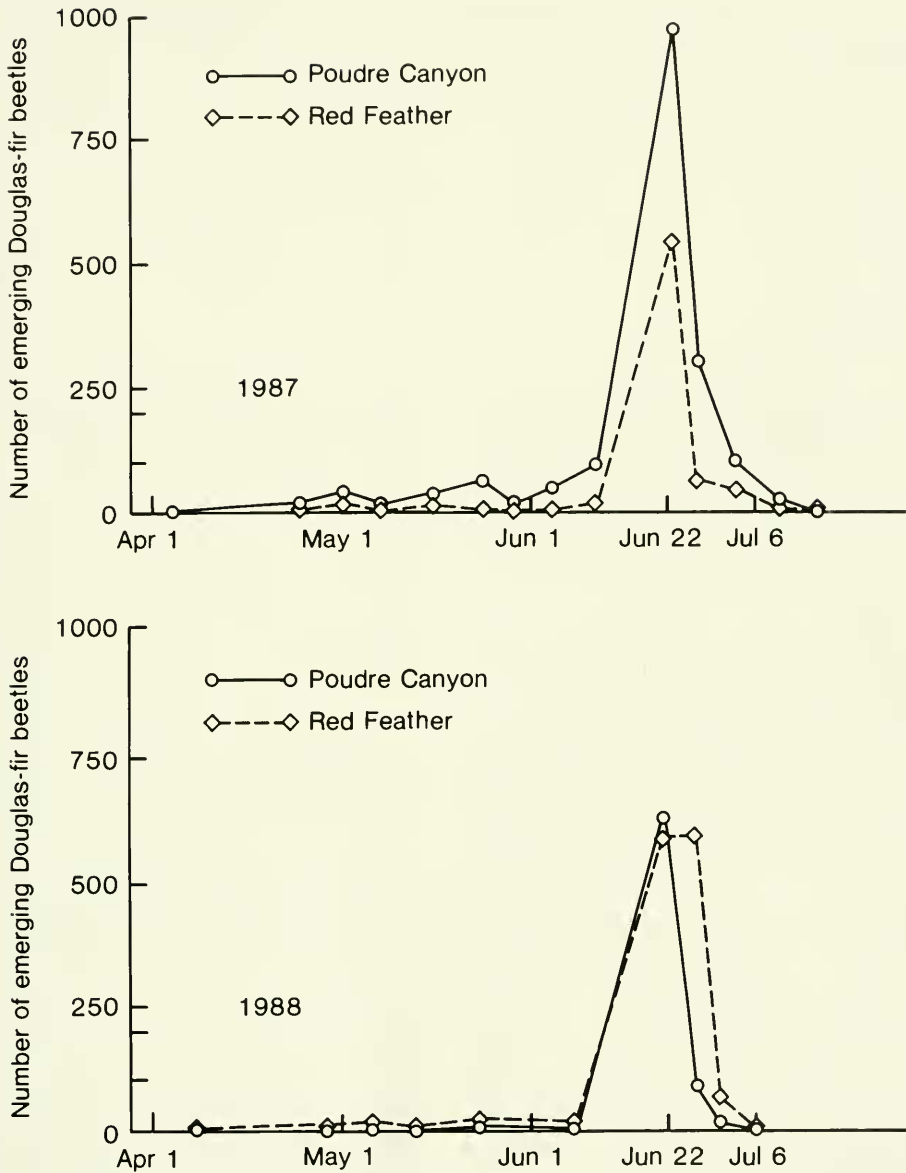
Fig. 1. Total number of Douglas-fir beetles emerging from five trees at four locations in the Arapaho-Roosevelt National Forest, Colorado, in 1987 and 1988.

the variability in site and stand conditions would not yield meaningful results in a more complex statistical design testing for differences among locations and their interactions. Periodic growth for the five-year periods was also used to compute Mahoney's PGR (Mahoney 1978), which is the ratio of the growth for one five-year period to the growth for the previous five years.

When analysis of variance indicated signifi-

cant differences among the means, Tukey's test was used to determine which means were different (alpha = .05) (Steel and Torrie 1960).

RESULTS AND DISCUSSION

EMERGENCE.—Adults began emerging in mid-April of both years (Fig. 1), continuing to emerge at low rates until early June. Emergence peaked between 10 and 26 June in both

Table 1. Mean number of Douglas-fir beetles emerging per sq. ft. (.09 m²) of bark for several locations in the Arapaho-Roosevelt National Forest. Within the same year, means followed by the same letter are not significantly different (alpha = .05).

Location	Number of trees		Cages per tree	Number of beetles ($\bar{x} \pm$ S.D.)	
	1987	1988		1987	1988
Narrows	5	2	2	27 ± 14 a	
Pingree Park Road	5	2	2	40 ± 20 a	
BM 6998	5	5	2	21 ± 15 a	30 ± 28 ab
Crystal Lakes	5	5	2	39 ± 18 a	55 ± 33 a
Camman Spring		5	2		8 ± 10 b
Black Mountain		5	2		10 ± 11 b

years. Adults rarely emerged after 1 July. In terms of percentage of the emerging populations, 18% of the beetles had emerged by 10 June in 1987 and 4% in 1988; 77% and 92% emerged between 10 and 26 June in 1987 and 1988; 5% and 4% emerged after 26 June, respectively. After 1 July, 2% or less emerged in both years.

Wood (1963) noted two principal flight periods for the Douglas-fir beetle in California, Oregon, and Utah, depending on the overwintering life stage—one during May–June and another during July–August. In this study we found only one principal flight period. If a second flight period is occurring, we believe the beetles are reemerging adults, not new adults emerging later from the caged hosts.

Density of emerging adults.—The number of adults emerging per sq. ft. (.09 m²) of bark surface ranged from 6 to 82 in 1987 and 0 to 88 in 1988. Mean numbers per sq. ft. (.09 m²) of bark showed significant variation among areas in 1987 and 1988, but Tukey's test did not reveal significant pairwise comparisons in 1987 (Table 1).

Although the number of emerging beetles did not significantly correlate with DBH, areas where mean tree diameter was 8.5 inches (22 cm) or less produced the lowest number of beetles. In addition, numbers were influenced by the density of attacks and tree diameter. The population trend ratio was generally >1 when attack densities were ≤12 per sq. ft. (.09 m²) and tree diameter was >10 inches (25 cm) DBH. When tree diameter was <10 inches (25 cm), the trend ratio was <1. Similarly, when the density of attacks was >14 per sq. ft. (.09 m²), the trend ratio was generally <1. Population trend thus appears to be influenced by competition (McMullen

Table 2. Mean number of Douglas-fir beetles emerging per sq. ft. (.09 m²) of bark by diameter class. Within the same year, means followed by the same letter are not significantly different (alpha = .05).

Diameter class (inches [cm])	Number of trees	Number of beetles ($\bar{x} \pm$ S.D.)
	1987	
7.5 – 9.6 (19–24)	5	21 ± 15 a
11.2 – 15.7 (28–40)	7	36 ± 16 a
16.2 – 24.3 (41–62)	8	34 ± 21 a
	1988	
9.3 – 12.5 (24–32)	6	22 ± 25 a
12.6 – 13.3 (32–34)	7	20 ± 20 a
13.4 – 18.0 (34–46)	7	35 ± 38 a

and Atkins 1961) and quantity of food (tree size, not number of trees) as hypothesized by Wright et al. (1984). Larger trees provide adequate food to produce an increasing population until the attack density exceeds 12 per sq. ft. (.09 m²). At greater densities, competition causes beetle production to decrease. Smaller trees generally have production rates less than one, even when attack densities are 8–12 per sq. ft. (.09 m²), because smaller trees do not provide sufficient phloem for developing larvae.

Beetle densities in this study were about the same as or greater than those found by Fredericks and Jenkins (1988) in Logan Canyon, Utah. Beetle numbers of 21–22 per sq. ft. (.09 m²) in our diameter classes of 7–13 inches (18–33 cm) were comparable to the beetle numbers at 22–24 per sq. ft. (.09 m²) of Fredericks and Jenkins (1988). In trees of comparable diameters (i.e., 22 inches [56 cm]), beetle numbers of 34 per sq. ft. (.09 m²) (Table 2) in this study were slightly greater than the 22–24 per sq. ft. (.09 m²) of Fredericks and Jenkins (1988).

TABLE 3. Mean annual radial growth in .001 inch (.025 cm) for the periods 1972–76, 1977–81, and 1982–86 for the four 1987 locations. Within the same location, means followed by the same letter are not significantly different (alpha = .05).

| | Mean annual growth (.001 inch) ($\bar{x} \pm$ S.E.) | | |
Location	1972–76	1977–81	1982–86
Narrows	11 ± 1.0 a (28 ± 3)	12 ± 1.4 a (30 ± 4)	19 ± 1.3 b (48 ± 3)
Pingree Park Road	38 ± 2.3 a (97 ± 6)	30 ± 1.2 b (76 ± 3)	33 ± 1.2 ab (84 ± 3)
BM 6998	11 ± 0.9 a (28 ± 2)	7 ± 0.3 b (18 ± 1)	12 ± 1.8 a (30 ± 5)
Crystal Lakes	7 ± 0.6 ab (18 ± 2)	5 ± 0.3 b (13 ± 1)	8 ± 1.0 a (20 ± 3)

ATTACK DENSITIES.—The number of attacks per sq. ft. (.09 m^2) of bark surface ranged from 8 to 20 in 1986 and 6 to 14 in 1987. Within each location, attack densities were not significantly different between aspects. Mean densities ranged from 9 to 15 in 1986 and 8 to 10 in 1987, comparable to the fifth-year attack densities in Oregon of Wright et al. (1984). Because the Colorado outbreak appeared to be in its fifth year, the pattern of attack densities during the outbreak may be the same as in the Oregon outbreak. In contrast, attack densities from our Colorado locations were 62–80% lower than those of the Utah outbreak. In the recent outbreak in Utah, attack densities were high and essentially the same throughout the first three years (Fredericks and Jenkins 1988). Apparently, the Utah outbreak exhibited a pattern of attacks different from either the Oregon or Colorado outbreaks.

DISCOLORATION OF INFESTED TREES.—In February following the attack, foliage of most infested trees was predominantly green, only the lower two or three whorls of branches having discolored to red-brown. By late April most trees had discolored, the color ranging from yellow-green to reddish. By mid-May most trees were reddish. Trees with extensive woodpecker debarking and foliage discoloration in February turned reddish first, usually by late April. Those without these characteristics discolored later but had turned by May. Foliage usually discolored at different rates in different crown levels, the lower crown fading first. When it was yellow-green, the rest of the crown was green. When the upper crown yellowed, the lower crown was already reddish. From August through October, the best external clues for Douglas-fir beetle infestation were cinnamon-colored boring dust and/or clear pitch "streamers."

During winter the most notable external characteristic was the debarked bole caused by woodpecker activity. These boles are lighter in color and can be discerned from more than 100 feet away. After October, but before the foliage turned red, woodpecker activity was the best characteristic for locating currently infested trees.

ANNUAL GROWTH.—Annual radial growth varied significantly among and within locations. Significant variation in growth among locations was expected because of differing site conditions, stand densities, and tree ages. In three of four locations, mean annual growth declined significantly in the 1977–81 period, presumably a result of the budworm outbreak (Table 3). Mean annual radial growth in each location increased during 1982–86. Thus, the increase in Douglas-fir beetle populations coincided with increasing growth of the host.

Mean annual growth for the 1977–81 period ranged from .005 inch to .03 inch (.013 to .08 cm) and for 1982–86 from .008 to .033 inch (.02 to .08 cm) (Table 3). The growth rate was greatest on large trees situated in a ravine, a more favorable site.

The periodic growth ratio (PGR) exhibited changes similar to the changes in mean annual radial growth. In three of four locations, PGR became <1 when 1977–81 was compared against 1972–76. PGR then became >1 when 1982–86 was compared with 1977–81. Growth rates declined for 1977–81 because of the budworm defoliation; thus, the change in PGR for 1977–81 vs. 1972–76 was expected. However, the increase in Douglas-fir beetle populations with >1 PGR for the 1982–86 period was unexpected. Most stands susceptible to the mountain pine beetle (*D. ponderosae* Hopkins) exhibit PGRs <1, and so a beetle outbreak coinciding with a period of increasing growth is unusual.

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